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# Capability of kittiwake and thick-billed murre to utilize the energy in capelin and Arctic cod

B. Brekke

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# CAPABILITY OF KITTIWAKE AND THICK-BILLED MURRE TO UTILIZE THE ENERGY IN CAPELIN AND ARCTIC COD

BY

BENTE BREKKE

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FOREWORD (p.4)

This major - subject thesis is financed by the Norwegian Research Council for Science and the Humanities (NAVF) and the Norwegian Polar Institute. It is a part of the project "Seabirds in the Arctic" which is a part of the research program Marine Ecological Research Program in the Arctic (Pro Mare). The results will be incorporated in a planned book where the work of Pro Mare will be summarized and recapitulated.

Geir W. Gabrielsen from the Norwegian Polar Institute has been a good guide for me. He has proposed a thesis in my major subject that is clear and well laid out, supported and motivated me throughout the work, and always been available to discuss ideas and questions.

Halvor Holm from the Institute of Nutritional Physiology has been supervising the nutritional physiology section of the thesis, and Johan B. Steen has been the formal supervisor in the Division for General Physiology. They have both been helpful and involved in my work.

I am thankful for all the assistance I have been given in connection with methodology and criticism of the manuscript. Especially valuable assistance has been received from Johan B. Steen who tirelessly has read and commented on my drafts, and by Ashild Krogdahl from the Norwegian Agricultural University who on several occasions has helped me with technical problems.

The analyses were performed at the Division of Marine Biology, The University in Oslo (UiO) under the supervision of Roy Beba, Norwegian Institute for Water Research (NIVA) and at the Institute for Nutritional Physiology, University in Oslo, under the guidance of Aud Jörgensen.

The Norwegian Polar Institute placed an office (p.5) at my disposal in connection with preparing and writing this thesis. Mona Bendixen (The Norwegian Polar Institute) has prepared the illustrations.

It has been pleasant to work with the nice people at the Norwegian Polar Institute.

I would finally like to especially thank the birds that patiently let themselves be pestered and thereby made this study possible.

Oslo, February 28, 1989 Bente Brekke

SUMMARY

This study is part of the Pro Mare seabird project "Seabirds in the Arctic". One purpose of the project has been to gain knowledge about how much energy seabirds take out of the Barents Sea, and how much energy they re-distribute.

An important part of this is to study to what degree seabirds utilize the energy in what they eat.

In the present work the energy utilization of capelin and Arctic (Polar) cod by black-legged kittiwake and thick-billed murre on Svalbard was studied.

Ten birds of each species were held in captivity in individual cages. They were fed for about 20 days with capelin and Arctic cod.

The energy utilization of the different feeds was found by calculating the difference in energy between the feed intake and energy in guano for each bird per day. The calculations were based on analyses of feed and guano. The values for energy utilization were corrected for positive/negative nitrogen balance.

The nitrogen-corrected energy utilization, for kittiwake and thick-billed murre respectively, was 72.2% and 70.6% for the capelin and 81.2 % and 74.7% for the Arctic cod. The energy utilization increased with an increase of fat in the feed.

A fluctuating fat content in the feeds was the most probable reason for the variations in energy utilization. The results indicate that kittiwake and thick-billed murre have the same ability to utilize the energy of what they eat.

The nesting black legged kittiwakes and thick-billed murres in Svalbard can,in the period they feed their young (30 days), consume 7789 tonnes capelin or 12,891 tonnes Arctic cod. This consumption is respectively 2% and 10% of the capelin and Arctic cod resources in the Barents Sea in 1988.

During the period they feed their young, respectively 16% ($9.0 \times 10^9$ kJ) and 25% ($1.6 \times 10^{10}$ kJ) of the consumed energy in

capelin/Arctic cod was returned to the environment around the colonies in the form of guano. This quantity of guano contains respectively 1608 tonnes and 2811 tonnes of nitrogen ; enough to fertilize the annual Norwegian potato harvest of 450,000 tonnes.

# 1. INTRODUCTION

## 1.1 Background

The Barents Sea is a marine arctic ecosystem with high biological production. The steadily increasing exploitation of the resources in this ocean has led to imbalance in the ecosystem. This appears to be a threat to several animal species living there. For this reason it is important to gain increased knowledge of the composition of the ecosystem; not the least to the interaction between the organisms living there. With this knowledge it would be possible to manage the Barents Sea in such a way that conditions are made right for a new balance. This awareness has led to increased financial support for biological research in these areas.

## 1.2 The role of seabirds in ecosystems

Seabirds are of great importance for the transport of energy through marine ecosystems. They are large consumers of marine resources, and this places them in a competitive situation with humans (Furness 1978, Crawford and Shelton 1978, Croxall 1983). Brown and Nettleship (1982) found that the yearly consumption of capelin (Mallotus villosus) by seabirds in the waters around Newfoundland of about 250,000 tonnes was in the same order of magnitude as that taken by seals and whales in the same area. Croxall (1983) has carried out studies in Antarctic waters, and found that seabirds there had a yearly consumption (directly and indirectly (1)) of krill (Euphausia superba) of (p.7) 115 million tonnes. This is somewhat more than what is taken by whales, and ca. 2/3 of what is eaten by seals in the same areas (Grenfell and Lawton 1979 (in Croxall 1983)). Studies from the Bering Sea (Hunt et. al. 1981) indicate that the consumption of young Alaska pollock (Theragra chalcogramma) by seabirds in this

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1) Indirectly means that they eat animals that have eaten krill.

area is about 50% of the commercial fishery for adult pollock in the same area.

Seabirds are also an important link between the marine and the terrestrial ecosystem. Norderhaug (1970) found in his studies of dovekie (Alle alle) on Svalbard that they during the nesting season transport large quantities of energy and nutrients from the ocean to shore. This supply of fertilizer around dovekie colonies results in the growth of a rich vegetation, which again forms biotopes for different insect, bird and mammal species. The many seabird colonies on Svalbard thereby maintain a high vegetative production around the nesting sites (Eurola and Hakala 1977, Remmert 1980, Klekowski and Opalinski 1986).

## 1.3 Studies of seabirds in the Barents Sea

Some aspects of the ecology of seabirds in the Barents Sea have been studied earlier (f.ex. Belopol'skii 1957). In the last five years, the focus has been on different aspects of nutritional ecology and energetics of seabirds as a project in the larger study entitled "Marine Ecology Research Program in the Arctic" (Pro Mare). One of the objectives of the project has been to gain knowledge on how much energy and nutrients the seabirds take out of the Barents Sea and how much they re-distribute, to give us an insight into the role of the seabirds in the ecosystem. This will make us better able to consider the requirements of the birds, for example in the allocation of fish quotas in certain ocean areas.

The work that has so far been done under the "seabird project", has been summarized in the annual reports of (p.10) Pro Mare (1984-1987). In brief, the work has been concentrated on the most numerous species in the Barents Sea ecosystem. These are Black-legged Kittiwake (Rissa tridactyla), Northern Fulmar (Fulmarus glacialis), Thick - billed Murre (Uria lomvia), Dovekie (Alle alle) , Black Guillemot (Cepphus grylle) and Glaucous Gull (Larus hyperboreus).

Birds of the various species have been sampled throughout

the year for stomach analysis (food choice) and body composition (fat and protein) (Gabrielsen and Mehlum, unpublished). Energy analyses of stomach content have also been carried out to determine the energy content of the birds' food sources throughout the year (Gabrielsen and Mehlum, unpublished).

Resting metabolism at different temperatures (thermoneutral zone, lower critical temperature) and insulating abilities have been studied through laboratory trials for the six above mentioned species (Gabrielsen et.al. 1987, Gabrielsen and Mehlum, in press, Gabrielsen et.al., in preparation). This gives us knowledge on the energy requirements of the birds throughout the year.

Daily energy consumption in the nesting season has been studied in free-living kittiwakes, dovekies and black guillemots (adults and chicks) by the use of the "double-labelled water method" (Gabrielsen et.al. 1987, Gabrielsen and Mehlum, in press, Gabrielsen et.al. in prep.).

By taking as the basis the results of the birds'energy consumption and energy balance throughout the year, we can calculate how much energy they must take up from the food to cover their daily energy requirements. In order to calculate quantitatively how much this is equivalent to of the various food items the birds eat, we must know to what degree they utilize the energy in these food items.

The ability of Arctic birds to utilize what they eat has not been studied before, but several studies have been done on domesticated chickens (hens) and a few on seabirds in the Antarctic. Studies on chickens have yielded knowledge on the nutritional physiology of birds, while work with seabirds (p.11) in the Antarctic has largely yielded results of doubtful value because important experimental conditions have not been met in these studies (Dunn 1975, Cooper 1977, 1978 and 1980, Adams 1984).

## 1.4 My studies

In this study I have investigated the energy utilization in a) capelin and b) Arctic (Polar) cod (Boreogadus saida) by I) Black legged kittiwakes and II) Thick billed murres on Svalbard.

Kittiwakes and murres were chosen because they are among the most numerous species of seabirds in the Barents Sea area. They are easy to capture and easy to work with. They belong to two different seabird families, Laridae and Alcidae, and gather food from the sea with different strategies; thick billed murres dive while the kittiwakes catch their food on the surface. It is therefore interesting to compare these two species. Capelin and Arctic cod were chosen as the food because they are among the principal food items of kittiwakes and murres. Arctic cod is also a key species in the Arctic food chain (Lydersen et.al. 1985).

## 1.5 Approach

I. I wish to answer the following question:
How much of the energy in Arctic cod and capelin is being utilized by kittiwakes and murres?

Answers to the question were sought through the (p.12) following studies:

a - determination of the energy -and nutrient content (²) in feeds,

b - determination of the energy -, nitrogen - and carbon content of guano,

c - registration of changes in body weight during the feeding periods.

---

²) With "nutrient content" we mean fat, protein and water contents.

II. Based on these results , I then wish to show to what extent the degree of energy utilization can be used in a model by answering the following questions:

1 - How much energy is taken out of the Barents Sea by kittiwakes and murres?
2 - To what extent do kittiwakes and murres redistribute the energy in the Barents Sea in the form of guano?
3 - Has the work with models consequences for the management of resources in the Barents Sea?

# 2. MATERIALS AND METHODS

## 2.1 Biology of experimental animals

### 2.1.1 Black-legged Kittiwake

Kittiwakes are found in all northern oceans, and is the most plentiful gull in the Barents Sea (Norderhaug et.al.1977).

They usually nest in mountain cliffs along the coast, and form colonies from a few up to ten thousands pairs (Norderhaug et.al.1977). On Spitsbergen egglaying commences in the beginning of June (Roemer and Schaudin 1900, Le Roi 1911; in Belopol'skii 1957). The female and male sit on the eggs alternately for ca. 25 days, and the chicks are fed for a further 41 days (Belopol'skii 1957). They are able to fly when they leave the nest, and become independent of the parents shortly afterwards.

Kittiwakes gather their food from the surface layer of the sea (0 to 1 m ) (Belopol'skii 1957, Norderhaug et. al. 1977). They can not dive actively, and take primarily pelagic organisms, especially crustaceans and small fish (Cramp 1983, Norderhaug et. al. 1977). From Arctic areas it has been reported that they feed on Arctic cod, capelin, pollock (saithe), amphipodes (for. ex. Parathemisto spp.) and copepods (for ex. Calanus spp.; f.ex. Hunt et al 1981, Brown and Nettleship 1982, Gasto unpublished). Their choice of food is to a large extent dependent on the availability of the food animals throughout the year, and varies from year to year (Belopol'skii 1957).

### 2.1.2 Thick - billed Murre (Brunnich's murre)

The thick-billed murre is one of the most numerous Arctic seabirds in the Barents Sea (Norderhaug 1977).

They nest in large or small colonies in steep mountain cliffs on the outer coast. On Spitsbergen the first eggs are laid around the end of May -beginning of June (Senander 1900, Le Roi 1911: in Belopo'skii 1957). The eggs are laid on narrow rocky

shelves and the female and male alternate in sitting on the eggs for ca. 33 days (Belopol'skii 1957). After being fed for ca. 20 days, the young birds jump into the sea (Belopol'skii 1957). They can not fly, and are being cared for by the male until they can fend for themselves (Harris and Birkhead 1985).

As all other Alcidae, thick-billed murres dive for their food. They can search for food down to 180 m, but most dives (ca. 80%) are within 40 m (Kooyman 1989, in press). They take primarily pelagic crustaceans and small fish. Choice of food animals depends on the availability throughout the year and can vary between years (Belopol'skii 1957). Important food animals in Arctic waters include Arctic cod, capelin, Northern sand lance (Ammodytes hexapterus), pollock and various amphipod species, especially Parathemisto spp. (f.ex. Tuck 1960, Hunt et al 1981, Scneider and Hunt 1982).

## 2.2 Experimental conditions

### 2.2.2 Food

In studies of the degree of utilization of foods where the results are to be used in an ecological model, the food studied should be the same as the one the birds would have chosen in the wild. I have therefore chosen food fish of about the same (p.15) length and weight as fish found in stomach samples of kittiwakes and murres.

### 2.2.1 Nutritional balance

The basic conditions for being able to use the measurements are that the experimental animals are nutritionally balanced during the experiment, i.e. that the body weight and composition of the animals does not change to any extent during the experimental period.

If a bird over a period has had stable body weight and been in balance with respect to nitrogen, the body composition for

that period has not changed.

A bird will have nitrogen balance when it takes in enough food to cover nitrogen requirements. Nitrogen requirement is the quantity of nitrogen a bird must take in to avoid loss of body proteins. The nitrogen requirements are determined by factors such as nitrogen for feather formation, nitrogen for egg and/or sperm formation, nitrogen for growth and loss of nitrogen in urine.

Nitrogen balance was in this study measured as nitrogen retention ( N [3] intake per day$^{-1}$ (g) - N in guano day $^{-1}$ (g)). Since no consideration was given to nitrogen lost in the form of feathers, a positive nitrogen retention will not necessarily mean growth. Since the birds in this study were not actively growing and did not form eggs or sperm, a positive nitrogen retention can reflect a loss of nitrogen in the form of feathers.

Body weight was measured daily, and daily nitrogen balance was registered through determination of the nitrogen content in food and guano. Since daily loss of nitrogen in the form of feathers has not been studied in seabirds earlier, I have (p.16) chosen to use daily nitrogen loss in the form of feathers from values for nitrogen balance in chickens as reference. Chickens (hens) are about the same size as kittiwakes and murres, and has a continuous, uniform growth of feathers. They have an estimated loss of nitrogen in the form of feathers of 50 mg/kg $^{0.75}$ body weight per day when they are in nitrogen balance (Krogdahl, personal communication).

---

[3]) N stands for nitrogen.

## 2.3 Energy utilization

### 2.3.1 The energy in foods

The energy contents in fat, protein and carbohydrate, as determined by bomb calorimeter (Whittow 1986), are:

| | |
|---|---|
| Fat | : 38.91 (kJ $g^{-1}$) |
| Protein | : 22.59 (kJ $g^{-1}$) |
| Carbohydrate | : 17.51 (kJ $g^{-1}$) |

In bomb calorific measurements, the three types of food are oxidized completely, and the energy content measured as heat liberated. This is a valid measure of energy utilization by birds in metabolizing fat and carbohydrate. When protein is oxidized in birds, the end product is principally uric acid which still contains energy. This is excreted in the urine. For birds the utilizable energy content in protein is therefore 4.60 kJ $g^{-1}$ less than that obtained through bomb calorimetric measurements, which is 17.99 kJ $g^{-1}$ (Whittow 1986).

### 2.3.2 Energy utilization (p.17)

Birds cover their energy requirements by eating, but not all energy in the food can be utilized by them. The degree of utilization depends on the energy losses in digestion, absorption, metabolism and excretion. The extent of the energy loss is therefore dependent on the species' physiological mechanisms for these processes relative to the biochemical composition of the feed.

Utilizable energy for birds can be expressed as energy intake less energy in guano (Harris 1966). The degree of energy utilization has therefore been calculated as daily utilizable energy in percent of daily energy taken in by the formula:

$$\frac{(E_{in} - E_{out}) \times 100}{E_{in}}$$

where $E_{in}$ is the daily energy intake and $E_{out}$ is the daily energy content of the guano.

2.3.3 Nitrogen corrected energy utilization

If there is a net catabolism of body proteins during the trial period, the nitrogen balance ($N_{in} - N_{out}$) will be negative, and the calculated energy utilization will be too low. On the other hand, if there is a net anabolism of body proteins, the nitrogen balance will be positive and the calculated energy utilization will be too high. At nitrogen balance, it is assumed as a simplification that catabolism is equal to anabolism. By calculating the nitrogen balance, a correction can be made for the effect of a positive or negative nitrogen balance.

For each gram nitrogen lost or retained, a total of 36.5 kJ is added or subtracted to/from the "utilizable energy". This value is the average energy content per gram (p.18) urine-nitrogen in birds (Titus et al 1959).

The degree of energy utilization is corrected to nitrogen balance by the formula:

$$\frac{(E_{in} - (E_{out} + NR)) \times 100}{E_{in}}$$

where NR (nitrogen retention)= ($N_{in} - N_{out}$) x 36.5 kJ $g^{-1}$ N, where $N_{in}$ is grams nitrogen in feed quantity per day and $N_{out}$ is grams nitrogen in guano per day.

2.3.4 Feces-metabolic and urine-endogenous energy

Harris defined in 1966 the term "true metabolizable energy" (TME) which is utilizable energy corrected for feces-metabolic and urine-endogenous losses. "Apparent metabolizable energy"

(AME) is utilizable energy without correction for feces-metabolic and urine-endogenous losses. AME and TME can in addition be corrected to zero nitrogen balance ($AME_n$ and $TME_n$). $TME_n$ is considered to be the most correct value for utilizable energy. Energy utilization without and with nitrogen correction (which is what I have calculated in the present study) is respectively AME and $AME_n$.

$AME_{(n)}$ and $TME_{(n)}$ converge with increasing food intake, i.e. that metabolic and endogenous losses in faces and urine has decreasing importance with increasing food intake (Wolynetz and Sibbald 1984). At low food intake it is therefore especially important to consider feces-metabolic and urine-endogenous losses. However, if the birds are fed at maintenance levels, these losses become less important. For example, the difference between TME and AME will be around 3% in mallard (Anas platyrhynchos) if they are fed on a maintenance level, while AME can be up (p.19)
to 40% lower than TME if the food intake of the birds is lower than maintenance level (Miller and Reinecke 1984).

In the present work the birds are fed at maintenance level, and I have therefore not considered feces-metabolic and urine-endogenous losses.

## 2.4 Field work

### 2.4.1 Location, climate

The field work was carried out in New - Aalesund (78°55'N, 11°59'E) on Svalbard in the periods July 8 to 29, 1985 (kittiwakes) and June 26 to July 18, 1986 (thick-billed murres). All birds were collected from the same cliff.

Average daytime temperature in the 1985 period was 6.8°C (± 1.4°C), the minimum temperature was 3.8°C and the maximum temperature 13.5°C. Average daytime temperature in the 1986

period was 5.2°C (± 1.8°C), minimum temperature was 0.6°C and maximum temperature 9.8°C. (The numbers in parenthesis are standard deviation).

2.4.2 Practical execution

Ten nesting kittiwakes and ten nesting murres of undetermined sex and age were captured on the nest by the help of a long fishing rod with a noose of fishing line at the end. They were placed in individual cages (50 cm x 60 cm x 60 cm) where they had an opportunity to drink seawater. The size of the cages permitted limited activity, but the birds were quietly lying down in a corner most of the time. The cages were placed outdoors in a place with low human activity, and was protected from rain (p.20) with a transparent, colorless tarpaulin. This gave the birds natural light - and temperature conditions and minimum disturbances. The cages had plastic covered chicken wire in the floor, front and roof. Plastic covered chicken wire makes the birds less exposed to damaging themselves (torn-off claws, skin scratches etc.), and the guano glides easily through the meshes without sticking.

A loose, plastic covered tray for collecting the guano was mounted under each cage. This was changed each morning at 09:00. The guano from each bird was transferred to previous weighed dishes, dried at 60-80° C to constant weight, and excreted dry matter per day was determined (Mettler PE 1600 0-1600 g (± 0.01 g)). The dry guano samples were homogenized with a mortar and pestle and frozen in separate plastic bags labelled with date and the number of the bird.

Two feeding experiments were carried out, one with each of the two seabird species. In the first period the birds were fed with capelin, in the second with Arctic cod. Each of the experimental periods were started by feeding for three to four days without collecting the guano to give the birds a period to adapt to the feed. Data were then collected over a period of from three to six days. The two experimental periods were carried out

without any waiting period between (see figures 2 and 3, page 31,32). Birds that injured themselves or in other ways could not be used for the experiments (for example if they threw up the food) were released before the planned experimental period was over. Among the kittiwakes, six participated in the whole study, four were released after the capelin period, and two new ones were captured for the Arctic cod period. Five thick-billed murres participated in the whole study, four were released after the capelin period, and one was released a couple of days after capture because it would not take any food. At the end of the experimental period, all the birds were released after being washed and dried, if necessary.

The murres were fed newly caught Arctic cod that were (p.21) stored in a refrigerator. Frozen capelin and Arctic cod that had been caught in the Barents Sea earlier in the year were used for the other experimental periods. The capelin used in 1985 and 1986 were caught in May the same year, while the catch date for the Arctic cod used in 1985 is unknown. The fish were taken out of the freezer at night and used the following day.

The birds were weighed each day at 08:00 (Mettler PE 16, 0-16 kg ($\pm$ 0.1 g)), and daily amounts of feed for the various birds were determined on the basis of changes in body weights from the day before. Daily feed portions were weighed in the morning (Mettler PE 1600, 0-1600 g ($\pm$ 0.01 g)). Four kittiwakes and four murres fed on their own and were given food 1-2 times a day, the rest were hand fed 4-8 time a day.

An analytical sample was taken of the feed each day, and random samples of fish (n=16-20) from the feed were measured and weighed in order to compare the size of the fish fed with the size of the fish the birds would feed on under natural conditions.

All feed- and guano samples were transported in the frozen state to Oslo where they were kept in a freezer (-20°C) until further processing.

## 2.5 Chemical analyses

The following analyses were performed on the feed:

- Water content
- Carbon- and nitrogen content
- Fat content
- Energy content

The following analyses were performed on the guano samples: (p.22)

- Carbon- and nitrogen content
- Energy content

It was found justifiable to use two or three parallel samples in most of the analyses since the parallels did not differ widely from each other.

### 2.5.1 Feed

Feed samples were taken in each of the four experimental periods, and these were homogenized (Ultra turax type T 45, 10,000 revs/min ). Samples were taken of the homogenates to determine the content of energy, water, fat,nitrogen and carbon.

Water and energy.

Three samples (7-10 gram) of each of the four homogenates were weighed in pre-weighed plastic bags (Mettler AE 100, 0-109 g (+/- 0.1 mg)). The samples were then freeze dried (HETOSICC type CD 52) for determination of water content.

The energy contents in the dry samples + plastic bags, and also the energy content per gram of the plastic (n=9) were determined by bomb calorimetry. The energy in the plastic was then subtracted to determine the energy content of the homogenates.

All energy determinations in this study was carried out with a Gallenkamp Autobomb (Automatic Adiabatic Bomb Calorimeter).

Fat.

Two to three samples of ca. 20 g of each homogenate were weighed (Mettler B 6, 0-100 g (± 0.1 mg)), and the fat content determined by extracting according to a modified Folch (p.23) method ( first extraction with chloroform:methanol in the proportion 2:1, separating the phases by adding physiological saline, and evaporating the organic phase in a rotavapor; Holm et al 1973). The fat was transferred to a weighing glass with the help of ether, and weighed after evaporation of the ether (Mettler AE 100, 0-100 g (± 0.1 mg)).

Nitrogen and carbon by elemental analysis

One to three mg (three parallels) of freeze dried homogenate was weighed and packaged in tin capsules (Mettler ME 30, 0-30 mg (± 1 g)). The tin capsules were washed once in chloroform and three times in 96% ethanol to remove impurities of carbon and nitrogen. Total contents of nitrogen and carbon were then determined (Elemental Analyzer CHN mod. 1106 (Carlo Erba Strumentazione) connected to an LDC model 308 Computing Integrator; sulfanilamide was used as standard.

2.5.2 Guano

All guano samples were freeze dried (HETROSICC type CD 52) before analysis to remove moisture picked up in transport and storage.

Energy.

The energy content was determined in an arbitrary selection of guano samples (three individuals from each group, 4-6 samples from each individual). Two tablets, each about one gram, were struck from each sample, weighed (Mettler AC 88, 0-88 g (± 0.1 mg)), and the energy content in these determined by bomb calorimetry.

Nitrogen and carbon. (p.24)

The nitrogen and carbon content was determined in each bird's daily guano by the same method as the two elements were determined in the feed samples (see above). Two parallel samples 0.5-1.5 mg each were weighed from each homogenate.

## 2.6 Processing of data

### 2.6.1 Mathematical calculations

For most of the mathematical calculations I have used the Lotus spreadsheet program (IBM program).

The protein content in feeds was calculated from the percentage nitrogen by the use of the conversion factor 6.25 (FAO/WHO 1973).

The percentage ash in feed was determined by difference: 100%- (%$H_2O$ + %lipid +% protein).

Daily nitrogen- and carbon excretion was calculated from the content of carbon and nitrogen in the daily sample, while daily energy excretion was calculated from the average content of energy in the guano in the different experimental periods. The following variables were then calculated per day for each bird: nitrogen-, carbon- and energy intake; nitrogen-, carbon- and energy excretion; nitrogen-, carbon- and energy retention; nitrogen retention as a percentage of nitrogen intake and energy utilization with and without nitrogen correction.

### 2.6.2 Statistical calculations and analyses

For the statistical calculations I used the program Statgraphics (IBM program).

Average values and standard deviations/errors are calculated according to the following pattern:

1) Averages and standard deviations (s.d) of all (4) variables are calculated for each bird per day through the various experimental periods.
2) Averages and standard errors (s.e) of the values generated under point 1), are calculated for all variables per species through the various experimental periods.

In parentheses, after each average value given, the following are shown: 1) s.d or s.e. and also 2) range of variation.

Probabilities of differences between the experimental groups are calculated with two-way Mann-Whitney U-test (non-parametric method).

Significant differences between the groups for $p \leq 0.05$. Tendency for correlation in the material for $0.1 \geq p \geq 0.05$. No significant difference for $p > 0.1$ (shown as n.s.).

Spearmans correlation analysis (non-parametric) is used to investigate the probability of dependence between parameters.

Significant correlation for $p \leq 0.05$. Tendency for correlation for $0.1 \geq p \geq 0.05$. Not significant correlation for $p > 0.1$ (shown as n.s.).

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4) - with the exception of values for nutritional contents in feeds and the body weights of the birds when captured.

## 3. RESULTS

(p.26)

The different experimental periods are from now on identified by a number:

I a) kittiwake fed with capelin,

I b) kittiwake fed with Arctic cod,

II a) thick-billed murre fed with capelin,

II b) thick-billed murre fed with Arctic cod.

### 3.1 Size of food animals

Table 1 shows the sizes of the capelin and Arctic cod used as feed in the two experiments. There were no significant differences in the lengths, but the weights were considerably higher for the Arctic cod than for the capelin. The Arctic cod was in other words "thicker" than the capelin.

Table 1 Total length and weight of feed animals

| Feed type | | Length (cm) | Weight (g) |
|---|---|---|---|
| K : Capelin | Ave | 10.4 | 3.7 |
| i : | s.d. | 0.7 | 0.8 |
| t : | n | 21 | 21 |
| t : | | | |
| i : Arctic cod | Ave | 13.2 | 14.2 |
| w : | s.d. | 1.3 | 4.3 |
| a : | n | 23 | 23 |
| k : | | | |
| e : | | | |
| M : Capelin | Ave. | 9.2 | 3.6 |
| u : | s.d. | 0.4 | 0.6 |
| r : | n | 20 | 20 |
| r : Arctic cod | Ave. | 9.9 | 7.7 |
| e : | s.d. | 2.2 | 7.1 |
| : | n | 16 | 16 |

It has been reported that kittiwakes and murres in the Svalbard area eat Arctic cod that have a length of respectively

3-19 cm (Mehlum and Gjertz 1984, Gjertz et al. 1985, (p.27) Lydersen et al 1985) and 3-18 cm (Lydersen et al 1985). I assume that kittiwakes and murres feed on this size class also with respect to other fish species. Therefore, the kittiwakes and murres were fed capelin and Arctic cod of the same size as the fish they feed on naturally.

## 3.2 Feed composition

The content of nitrogen, carbon and energy in the feed is shown in Table 2. The feeds had the same percentage content of nitrogen (protein), while the carbon content fluctuated in proportion to the energy content ($p \leq 0.04$). This relationship between energy and carbon is well known, and the amount of carbon can be used as a measure of the energy content (see Scheider and Hunt 1982).

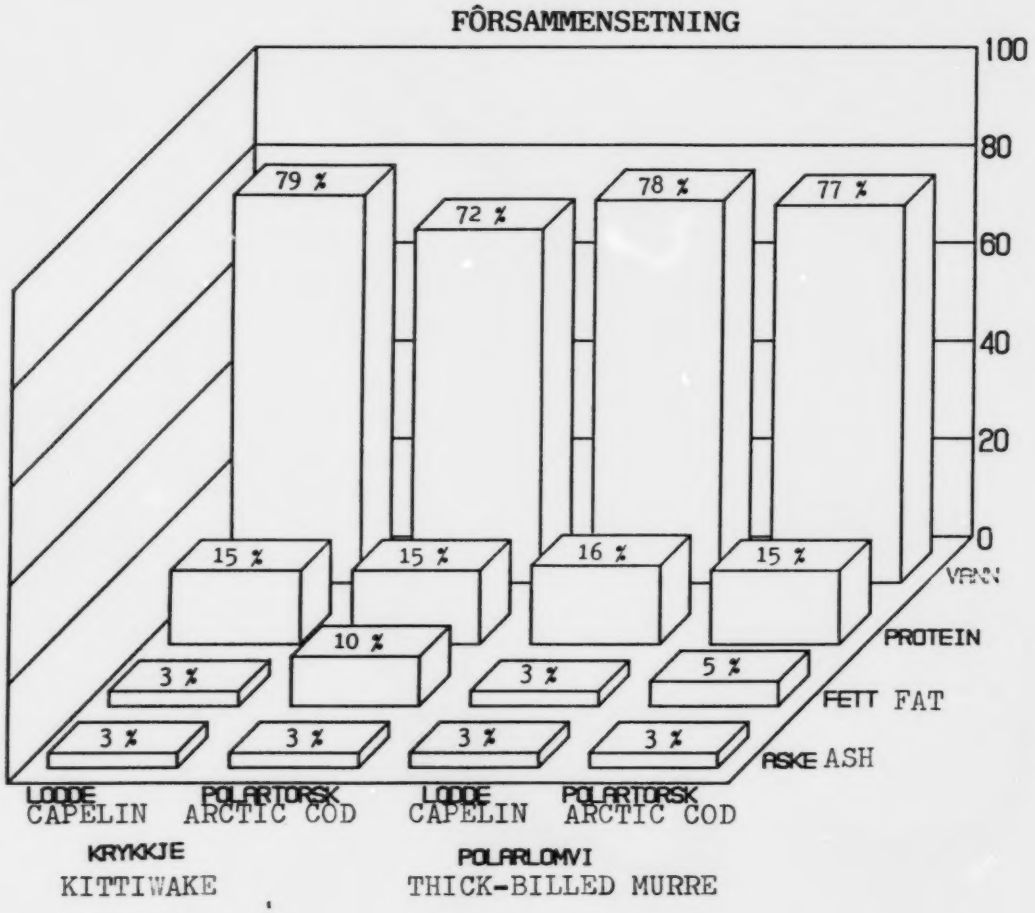
Table 2 Content of nitrogen, carbon and energy in the feed.

| | Feed type | | Nitrogen (%) | Karbon (%) | Energi ($kJ\ g^{-1}$ VV) | Energi ($kJ\ g^{-1}$ TV) |
|---|---|---|---|---|---|---|
| Kittiwake | Capelin | Ave | 2.38 | 9.19 | 4.1 | 20.1 |
| | | s.d. | 0.08 | 0.22 | 0.2 | 0.7 |
| | | n | 3 | 3 | 3 | 3 |
| | Arctic cod | Ave | 2.43 | 15.51 | 7.4 | 29.1 |
| | | s.d. | $6*10^{-3}$ | 0.14 | 0.07 | 0.3 |
| | | n | 3 | 3 | 3 | 3 |
| Murre | Capelin | Ave | 2.56 | 9.92 | 4.5 | 20.8 |
| | | s.d. | 0.02 | 0.14 | 0.06 | 0.3 |
| | | n | 3 | 3 | 2 | 2 |
| | Arctic cod | Ave | 2.34 | 10.91 | 4.9 | 21.9 |
| | | s.d. | 0.02 | 0.18 | 0.01 | 0.04 |
| | | n | 3 | 3 | 3 | 3 |

VV= wet weight TV= dry weight

The content of water, protein, lipid and ash in the feed (p.28) is shown in Figure 1.

FEED COMPOSITION




**Figur 1** **Innhold av vann, protein, fett og aske (% av våtvekt) i de ulike fôr. Standard avvik for vann-, protein- og fettanalyser er henholdsvis: lodde-krykkje: 0.04, 0.47, 0.06; polartorsk-krykkje: 0.01, 0.04, 0.06; lodde-polarlomvi: 0.12, 0.1, 0.22; polartorsk-polarlomvi: 0.04, 0.13, 0.01.**

Figure 1. Content of water, protein, fat and ash (% of wet weight) in the different feeds. Standard deviations for water-, protein- and fat analyses are respectively : capelin-kittiwake: 0.04, 0.47, 0.06; Arctic cod-murre: 0.01, 0.04, 0.06; capelin-murre: 0.12, 0.1, 0.22; Arctic cod:murre: 0.04, 0.13, 0.01.

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The two capelin feeds had about the same nutritional composition and energy content. The Arctic cod differed from the capelin by having a higher lipid-, energy- and carbon content and a lower water content. It therefore had higher energy density than the capelin.The polar cod that the murres were fed had a 5% higher fat content (therefore also a higher energy- and carbon content) than the Arctic cod the kittiwakes were fed. The fat content of the feeds was inversely proportional to the water content ($p \leq 0.04$).

Several studies of the seasonal variations in the nutrient composition of capelin have been carried out ( see Jangaard 1974, Eaton et al 1975, Montevecchi and Piatt 1984). Montevecchi and Piatt (1984) found in capelin around Newfoundland a constant protein content (13-14%) the year around, while the fat and water contents were inversely proportional. The highest fat content (18%)/ lowest water content (67%) were found in capelin in December, and the lowest fat content (3%)/ highest water content (81%) in June-July coinciding with the spawning period. Jangaard (1974) describes similar fluctuations for the capelin in the Barents Sea, and points out that the minimum value for fat content is reached immediately after the fish has spawned in April.

The capelin used as feed, both samples collected in the Barents Sea in May, contained 3% fat and 70-80% water. The protein content was about 15-16%. These values are in agreement with the above mentioned results from Montevecchi and Piatt(1984) and Jangaard (1974).

No publications on similar studies on Arctic cod are available. Gabrielsen (personal communication) has carried out nutritional composition analyses of Arctic cod caught in the Barents Sea in February-March, May and August. The fat content was in the different periods respectively 10%, 4% and 6%. The protein content was in February-March and in August around 13-14%, while it was down to 7% in May.

The Arctic cod in the present study which was caught in July

had a somewhat lower fat content than the above mentioned value from August, something that seems to indicate that the fish in this period is becoming fatter since the food supply at this time is increasing. The other Arctic cod fed had a fat content of 10%, close to the above-mentioned value from February-March, and can have been caught in this period. The protein content was around 15% - somewhat higher than in Gabrielsen's studies.

3.3 Feed intake (p.30)

Average feed intake for each day throughout the experimental periods is shown in Figures 2a and 3a. The figures show that the feed intake for both bird species increased throughout the capelin period, and declined through the Arctic cod period. The average, daily feed intake was in the experimental period Ia, Ib, IIa, and IIb respectively 141.4 g capelin ($\pm$ 19.5 g, 118.7 - 163.8 g), 106.4 g Arctic cod ($\pm$ 12.1 g, 96.3 - 110.7 g), 278.9 g capelin ($\pm$ 24.3 g, 246.7 - 331.8 g) and 267.1 g Arctic cod ($\pm$ 35.7 g, 242.4 - 307.9 g).

The kittiwakes had a higher average daily intake of capelin than of Arctic cod ($p \leq 0.005$), while the thick-billed murres did not have a significant different feed intake in the two experimental periods.

3.4 Guano composition

The content of nitrogen, carbon and energy in guano from kittiwakes and thick-billed murres fed with capelin and Arctic cod is given in Table 3.

The probability of differences between all combinations of values within the groups 1) nitrogen content, 2) carbon content and 3) energy content was tested. Significant differences and tendencies for significant differences were found between some combinations within the groups, but there was no consistency between the groups (Appendix 1). It can be seen in Table 3 that any differences are small.

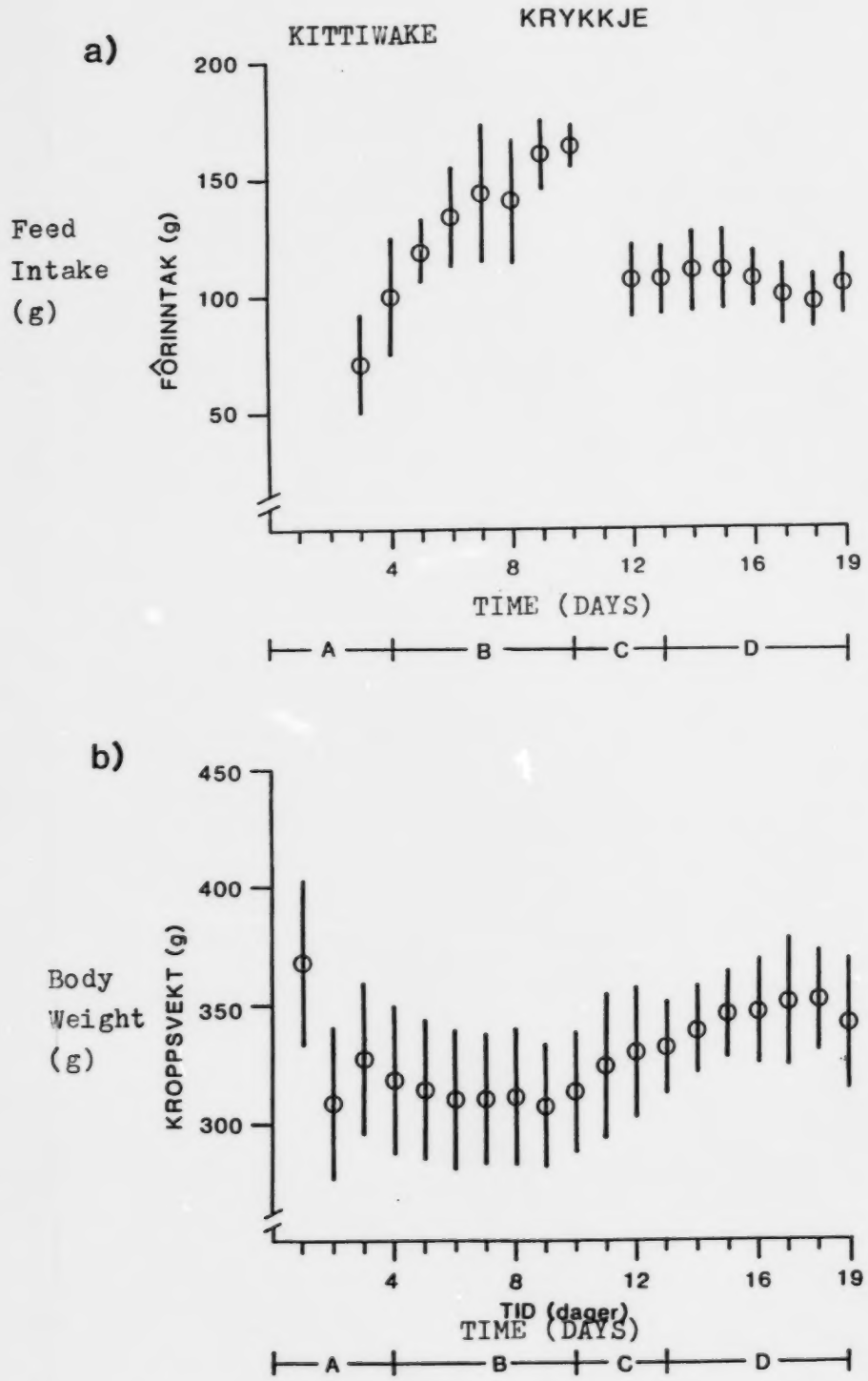



Figure 2 a) Average feed intake and b) average body weight for each day for kittiwake throughout the experimental period. The periods A and C (under the X-axis) are adaptation periods to respectively capelin - and Arctic cod feeds. In the periods B and D, data were collected for studies of the energy utilization of respectively capelin and Arctic cod.

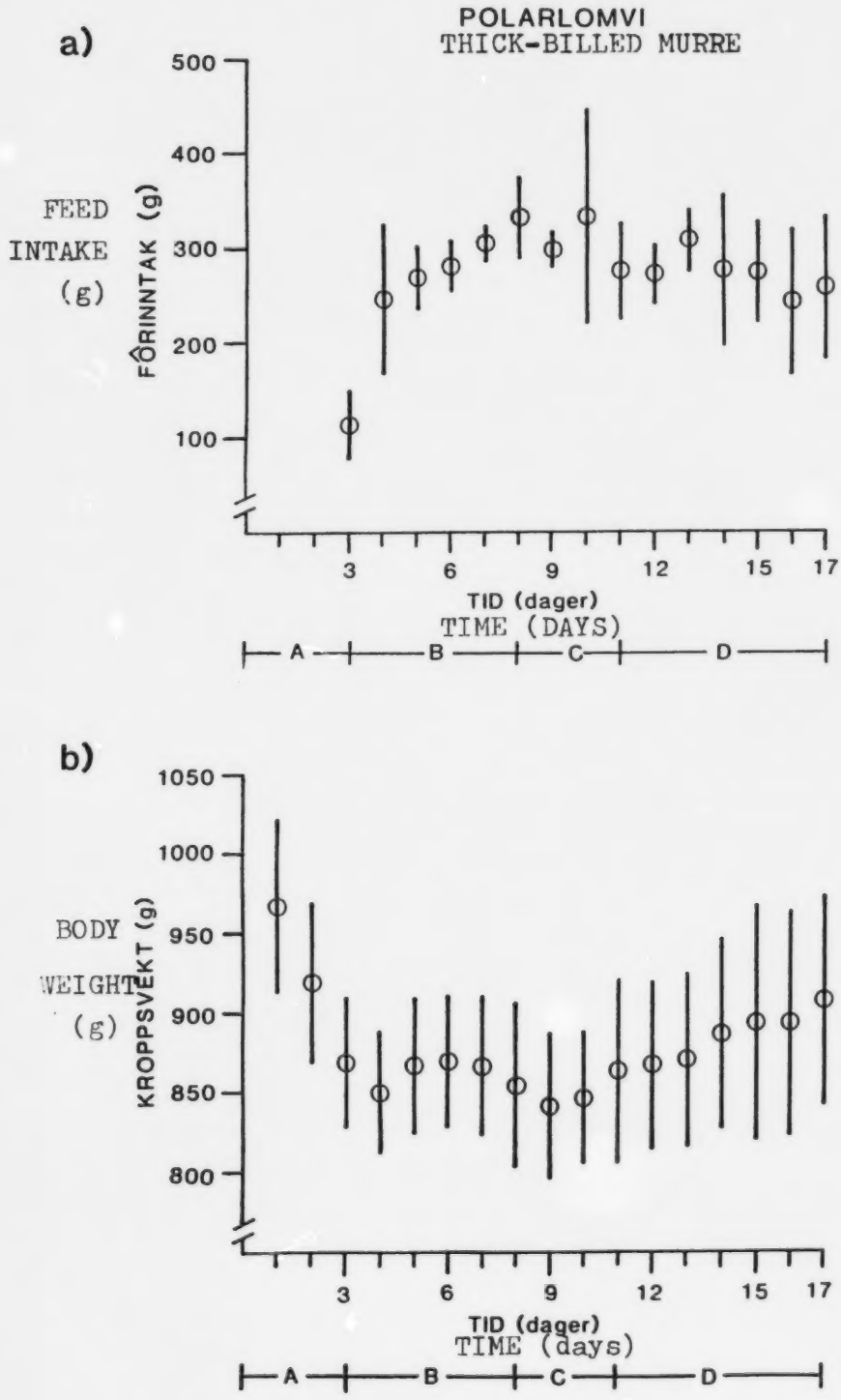



Figure 3 a) Average feed intake and b) average body weight of thick-billed murres for each day throughout the experimental period. The periods A and C (under the X - axis) are adaptation periods for respectively capelin- and Arctic cod feeds. In the periods B and D, data were collected for studies of the energy utilization of respectively capelin and Arctic cod.

Table 3 Content of nitrogen, carbon and energy in guano.

Tabell 3 Innhold av nitrogen, karbon, og energi i guano.

| | Fôrtype / Feed | | Nitrogen (%) | Karbon (%) | Energi (J $g^{-1}$ TV) |
|---|---|---|---|---|---|
| KITTY_WAKE | Lodde / Capelin | snitt (ave) | 22.24 | 29.42 | 11607 |
| | | s.e. | 0.54 | 0.49 | 83 |
| | | n | 10 | 10 | 3 |
| | Polartorsk / Arctic cod | snitt ave. | 20.05 | 30.16 | 12191 |
| | | s.e. | 0.63 | 0.40 | 177 |
| | | n | 8 | 8 | 3 |
| Murre | Lodde / Capelin | snitt | 21.57 | 30.04 | 11959 |
| | | s.e. | 0.57 | 0.56 | 96 |
| | | n | 9 | 9 | 3 |
| | Polartorsk / Arctic cod | snitt | 20.64 | 29.51 | 11727 |
| | | s.e. | 0.99 | 0.26 | 285 |
| | | n | 5 | 5 | 5 |

TV= tørrvekt TV = dry weight

## 3.5 Guano quantities

The average daily quantities of guano (dry weight) from kittiwakes and murres in the experimental periods Ia, Ib, IIa IIb were respectively 11.4 g (± 1.8 g), 10.9 g (± 1.6 g), 16.7 g (± 2.6 g) and 25.1 g (± 5.2g).

## 3.6 Changes in body weight

The average body weight at capture was for kittiwakes 366 g (± 35 g) and for thick-billed murres 967 g (± 54 g). Average body weights throughout the experimental period are given in Table 4.

Table 4 Average values of body weights throughout the experimental periods.

| | Kittiwake | | Thick-billed murre | |
|---|---|---|---|---|
| Feed: | Capelin | Arctic cod | Capelin | Arctic cod |
| Ave. | 312 | 347 | 864 | 884 |
| s.e. | 28 | 21 | 41 | 63 |

It was not possible to keep the body weights absolutely stable. Figure 2b an 3b show that the birds lost weight the first three-four days after capture. This weight loss was on an average 14.7% (± 3.1%) of the original body weight for kittiwakes and 12.1% (± 2.2%) for thick-billed murres. The average daily change from then on, as a percentage of yesterday's weight, was zero for kittiwakes that ate capelin, and between 0.5% and 1% in the other groups (Table 5). When the feed was changed from capelin to Arctic cod, the birds had a definite body weight increase of around 6%. As a result, the body weights of both kittiwakes and murres were higher in the Arctic cod period than in the capelin period ($p \leq 0.01$).

Table 5 Average daily changes in body weights.

| | Kittiwakes | | Thick-billed murres | |
|---|---|---|---|---|
| Feed: | Capelin | Arctic cod | Capelin | Arctic cod |
| Ave | 0.0 | 1.0 | 0.7 | 0.6 |
| s.e. | 0.7 | 0.6 | 0.4 | 0.7 |

## 3.7 Utilization of nutrients

### 3.7.1 Nitrogen, carbon and energy

Table 6 shows average daily intake, excretion and retention of nitrogen, carbon and energy per bird in the four experimental periods. Both bird species had greater retention of (p.35) carbon and energy and lower retention of nitrogen in the polar cod period than in the capelin period.

Table 6 Average total quantities of nitrogen, carbon and energy taken in (I), excreted (E) and retained (R) per day per bird in the different experimental groups.

| | | | KRYKKJE KITTYWAKE | | | | | |
|---|---|---|---|---|---|---|---|---|
| Fôrtype Feed | | | Lodde Capelin | | | Polartorsk Arctic cod | | |
| | | | I | E | R | I | E | R |
| Nitrogen (gram) | snitt | ave | 3.4 | 2.5 | 0.8 | 2.6 | 2.2 | 0.4 |
| | s.e. | | 0.5 | 0.4 | 0.2 | 0.3 | 0.3 | 0.08 |
| | n | | 10 | 10 | 10 | 8 | 8 | 8 |
| Karbon | snitt | ave | 13.0 | 3.4 | 9.7 | 16.5 | 3.3 | 13.2 |
| | n | | 10 | 10 | 10 | 8 | 8 | 8 |
| Energi (J) | snitt | ave | 583.0 | 132.1 | 450.9 | 785.6 | 133.5 | 652.1 |
| | s.e. | | 80.4 | 21.6 | 60.9 | 89.5 | 19.6 | 70.3 |
| | n | | 10 | 10 | 10 | 8 | 8 | 8 |

| | | | MURRE POLARLOMVI | | | | | |
|---|---|---|---|---|---|---|---|---|
| Fôrtype Feed | | | Lodde Capelin | | | Polartorsk Arctic cod | | |
| | | | I | E | R | I | E | R |
| Nitrogen (gram) | snitt | ave | 7.1 | 5.8 | 1.4 | 6.2 | 5.1 | 1.1 |
| | s.e. | | 0.6 | 0.7 | 0.4 | 0.8 | 1.1 | 0.9 |
| | n | | 9 | 9 | 9 | 5 | 5 | 5 |
| Karbon (gram) | snitt | ave | 27.7 | 8.0 | 19.7 | 29.1 | 7.4 | 21.7 |
| | s.e. | | 2.4 | 0.8 | 1.8 | 3.9 | 1.6 | 3.2 |
| | n | | 9 | 9 | 9 | 5 | 5 | 5 |
| Energi (J) | snitt | | 1262.1 | 319.2 | 942.9 | 1319.6 | 295.7 | 1023.8 |
| | s.e. | | 109.9 | 31.2 | 84.7 | 176.5 | 61.0 | 147.0 |
| | n | | 9 | 9 | 9 | 5 | 5 | 5 |

Retained nitrogen as a percentage of body weight is given in Table 7. In the Arctic cod periods, the kittiwakes and murres retained the same quantities of nitrogen from the feed relative to their size (n.s.) The nitrogen retention in relation to size was for both species lower in the Arctic cod period than in the capelin period ($p \leq 0.0004$). In the capelin period , the kittiwakes had higher nitrogen retention in relation to (p.36) the body weights than the thick-billed murres.

Table 7 Nitrogen retention as percent of body weight (bird day $^{-1}$)

| Feed | | Kittiwake | Murre |
|---|---|---|---|
| Capelin | Ave. | 0.27 | 0.18 |
| | s.e. | 0.06 | 0.05 |
| Arctic cod | Ave. | 0.12 | 0.15 |
| | s.e. | 0.03 | 0.06 |

Retained nitrogen as a percentage of nitrogen intake is given in Table 8. "The utilization" of nitrogen (protein) was highest for the kittiwakes in the capelin period ($p \leq 0.001$). In the murres the difference between average "nitrogen utilization" in the two periods was 9%. This difference is not significant.

Table 8 Nitrogen retention as a percentage of nitrogen intake (bird per day $^{-1}$).

| Feed | | Kittiwake | Murre |
|---|---|---|---|
| Capelin | Ave. | 25.1 | 29.2 |
| | s.e. | 3.8 | 5.4 |
| Arctic cod | Ave. | 15.9 | 20.5 |
| | s.e. | 4.4 | 9.3 |

### 3.7.2 Energy utilization

The average energy utilization of the birds, calculated with and without nitrogen correction, is given in Table 9.

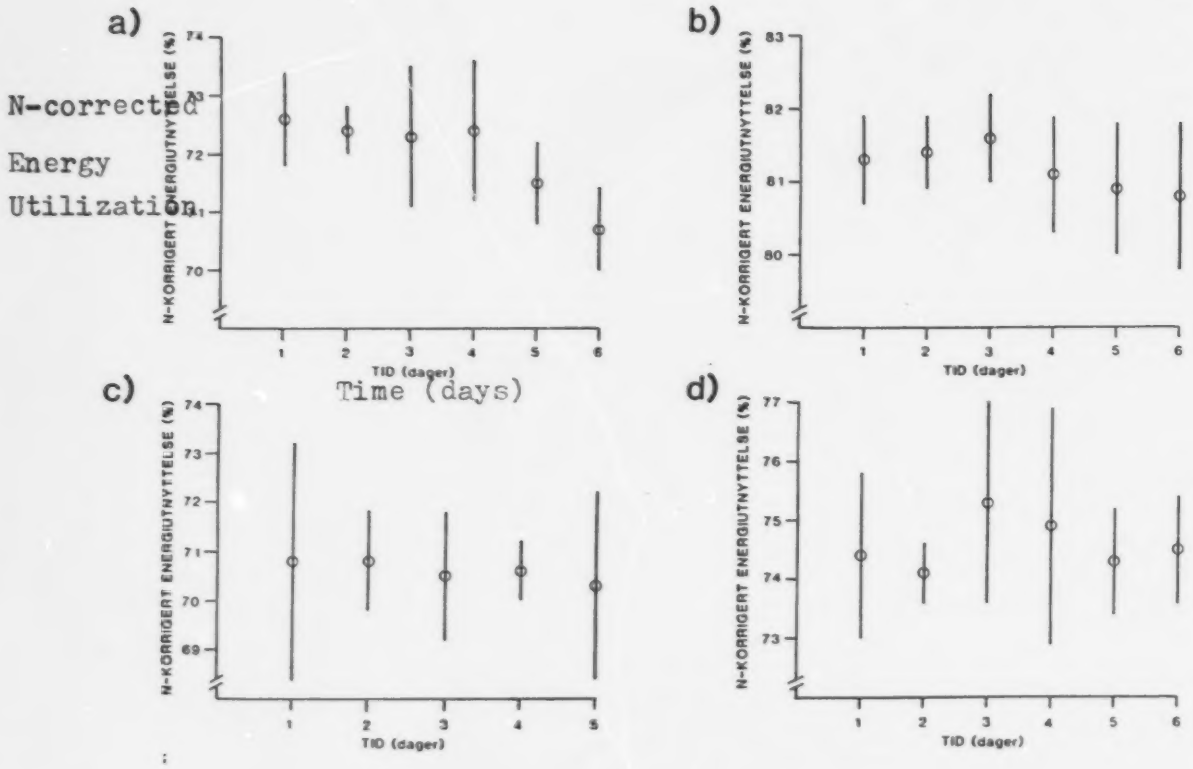
Table 9 Average energy utilization (EU) and nitrogen corrected energy utilization ($EU_n$) for kittiwake and murre for various feeds.

| | Feed | | EU (%) | $EU_n$ (%) |
|---|---|---|---|---|
| K | Capelin | Ave. | 77.5 | 72.2 |
| I | | s.e. | 1.4 | 0.7 |
| T | | n | 10 | 10 |
| T | | | | |
| I | Arctic cod | Ave. | 83.1 | 81.2 |
| W | | s.e. | 0.7 | 0.4 |
| A | | n | 8 | 8 |
| K | | | | |
| E | | | | |
| M | Capelin | Ave. | 74.4 | 70.6 |
| U | | s.e. | 1.6 | 0.6 |
| R | | n | 9 | 9 |
| R | | | | |
| E | Arctic cod | Ave | 78.2 | 74.7 |
| | | s.e. | 2.5 | 0.3 |
| | | n | 5 | 5 |

There was a significant difference between all combinations of the nitrogen - corrected degrees of utilization ($p \leq 0.011$).

Both kittiwake and thick-billed murre utilized the energy in Arctic cod better than they utilized the energy in capelin, and kittiwake utilized the energy in Arctic cod better than thick-billed murre. The difference in nitrogen corrected energy utilization between kittiwake and murre was small (1.6%). Taking into consideration that the experiments with the two bird species were performed in two different years, the difference can be due to a coincidence.

On average, the daily nitrogen-corrected energy utilization is shown in Figure 4. The variations from day to day were through all four experimental periods within two percent. This is assumed to be stable.




**Figur 4** Gjennomsnittlig, daglig nitrogenkorrigert energiutnyttelse for a) krykkje som spiste lodde, b) krykkje som spiste polartorsk, c) polarlomvi som spiste lodde, d) polarlomvi som spiste polartorsk.

Figure 4. Average, daily nitrogen corrected energy utilization for a) kittiwake fed capelin b) kittiwake fed Arctic cod c) thick-billed murre fed capelin, d) thick-billed murre fed Arctic cod.

# 4. DISCUSSION

(p.39)

## 4.1 Nutritional balance

### 4.1.1 Changes in body weight and nitrogen balance

Figures 1a and 2a show that the birds lost 12-15% of their original body weight in the first three-four days in captivity. At the conclusion of the experiment they had regained about half of this loss.

The initial drop in body weight is assumed to be a result of insufficient energy intake since increasing food intakes stabilized the body weight. A rapid and moderate reduction in body weight like this is primarily due to loss of water and reduction of fat reserves (Parker and Holm, unpublished), but some protein will also be lost if the energy intake is not high enough relative to the energy requirement over a somewhat longer period (Holm, personal communication).

A kittiwake loses about 17% of its original body weight during the nesting season (Gabrielsen, personal communication). At the start of the nesting season, the average fat content is 13-14% and the protein content 21-22 %. When the eggs hatch, the fat content has dropped to 9-10%, and it then remains stable until the chicks have left the nest. The protein content if fairly stable throughout the whole nesting season (Gabrielsen, personal communication). Kittiwakes can feed through the whole nesting season since the male and the female share in the work with eggs and chicks. Even if the weight drops during the summer, they take in enough energy and protein to avoid a large loss of body proteins. Preliminary studies of thick-billed murres in the nesting season indicate similar changes in this species (Gabrielsen, personal communication).

The nitrogen balance of the birds was positive (p.40) throughout the whole period in captivity. Their nitrogen retention was between 20 and 40 times as high as the estimated loss of nitrogen in the form of feathers in domesticated

chickens, which is 50 mg N/kg$^{0.75}$ body weight. Chickens (hens) of the same size as the kittiwakes in this experiment will have a loss of feathers corresponding to 0.02 g N day$^{-1}$, while the kittiwakes had an average nitrogen retention of 0.8 g N day$^{-1}$ in the capelin period and 0.4 g N day$^{-1}$ in the Arctic cod period. Chickens (hens) of the same size as the thick-billed murres will have a loss of feathers corresponding to 0.05 g N day$^{-1}$, while the murres retained an average of 1.4 g N day$^{-1}$ in the capelin period and 1.1 g N day$^{-1}$ in the Arctic cod period. This indicates that the birds had a loss of body proteins in connection with the low feed intake that caused the reduction in body weight.

This theory is also supported by the fact that the nitrogen retention, as a percentage of the body weight, was highest in the first half of the experiment for all birds. This indicates that the nitrogen requirements were reduced as feed intake, body weight and well being increased. That the kittiwakes in the first period had higher nitrogen retention as a percent of the body weight than the thick-billed murres, can be due to the fact that the kittiwakes had the highest initial weight loss (relative to the body size), and therefore a higher nitrogen requirement.

Low nitrogen retention in the last half of the experiment can be due to the fact that the protein intake was lower at that time than in the first half, and that the protein intake therefore was not high enough to cover nitrogen requirements. However, the feed intake at this stage of the experiment was voluntary for many of the birds, and there is therefore reason to believe that they ate what they required. That the birds to a certain extent had managed "to eat themselves up" already in the first experimental period, therefore seems most likely.

However, there is not anything about the results that indicate that the loss of body proteins was so drastic (p.41) that it affected the end results. For example, there was little difference in the contents of nitrogen, carbon and energy in the different experimental periods. This indicates that the physiological mechanisms of the birds with respect to digestion,

absorption, metabolism and excretion were stable throughout the experimental periods.

The thick-billed murres had in general higher nitrogen retention (in grams) than kittiwakes. This can simplest be explained by the size differential between the two bird species. Thick-billed murres are twice as big as kittiwakes and have therefore correspondingly higher nitrogen requirements.

### 4.1.2 Changes in body weight and feed intake

In spite of an increase in the feed intake, the birds had a stable body weight when being fed with capelin. In addition they also had a net synthesis of body protein in this period. They can therefore have lost fat and/or water, and as a result have had a change in body composition. There is nothing that indicated that this has affected the end results.

## 4.2 Energy utilization

Numerous studies have been published on the energy utilization of seabirds. Only in one of them (Jackson 1986) has consideration been given to the nitrogen balance of the birds by carrying out nitrogen correction of the energy utilization. Of earlier seabird studies, it is therefore only this one study that it is relevant to compare my results with.

### 4.2.1 Nitrogen correction of energy utilization (P.42)

Correction of the energy utilization values to zero nitrogen balance reduced them by 2-7%. In a study of the feed utilization in poultry of over 50 types of feed (410 experiments; Sibbald 1986), the degree of utilization was reduced by 0-14% through the correction to zero nitrogen balance. A reduction of 2-7% therefore seems to be acceptable considering the accuracy of the results.

Jackson (1986) obtained reductions of 6-11% by carrying out the same corrections in studied with "white-chinned" petrels (Pocellaria aequinoctialis). The birds in this study were chicks

just able to fly that went through several fasting periods, and as a results of this had a daily weight loss of 3.8% total body weight in the ten days the experiment lasted. The birds had as a result of this probably both sharply increased nitrogen - and energy requirements that led to increased nitrogen retention when they again were given food. As a result, the effect of the nitrogen correction was large.

The birds in my studies were adult birds that had not fasted, but that probably had a loss of body proteins in connection with the drop in body weight the first days after capture. Their nitrogen requirements were therefore increased, but to a lesser degree than in the birds in Jackson's study.

The correction of the energy utilization values of the nitrogen balance did not reduce the difference between them. On the contrary, in kittiwakes it led to larger differences in the degree of utilization of capelin and Arctic cod, while in thick-billed murre there was no change in the differences. This means that there were real differences in the utilization of feed within each individual and between the two seabird species.

An indication of this was that body weight of all birds increased during the adaptation period to Arctic cod in (p.43) spite of the fact that the feed intake was lower than in the previous capelin period for kittiwakes and stable for thick-billed murres. The kittiwakes reduced their feed intake by 25% while the body weight increased by 6.5 g (ca. 2%) per day. The murres had the same feed intake in both periods and a body weight increase of 3.3 g (ca. 0.4%) per day.

### 4.2.2 Cause of fluctuating energy utilization

In the poultry industry it is important that production is as high as possible at as low a price as possible. It is therefore of interest to find the combination of nutrients that give the best results relative to costs. The degree of utilization of various combinations of nutrients have been studied, and a number of sides of the nutritional physiology of

the birds have been clarified.

One study found that the energy utilization varied between different feed types, between different age groups within the individual species and between species (Sibbald 1982).

Seabird researchers have another reason for their studies. Their results are often used in ecological models, and the bird's normal food is used as feed.

Seabird researchers have commented on inter- and intraspecific variations in energy utilization (Cooper 1977, 1978, 1980; Heath and Randall 1985, Jackson 1986). However, in most of these studies no nitrogen corrections were performed, and the results are therefore associated with a high degree of uncertainty. Few seabird researchers seems to be interested in the reasons for the variations and none seems to have utilized knowledge from poultry research. Only in one seabird study (Jackson 1986), have theories been proposed on what the variations could be caused by.

Jackson (1986) suggests that the order of experimental series using different feeds can affect the degree of (p.44) energy utilization in the birds. Adaptation to a type of food can have short term effects on the utilization of other food types.

Longer adaptation - and experimental periods would expose an effect like this. The adaptation - and experimental periods in my work were longer than recommended (Sibbald 1982; also longer than in Jackson's studies), and the daily degree of energy utilization was approximately stable through the different experimental periods. It is therefore not probable that the differences in the degree of energy utilization in my experimental groups were short term effects.

Better energy utilization in the last rather than the first half of the experiment could be due to the fact that the birds had a longer time to adapt to being caged in the second (6-9 days adaptation) than in the first (3 days adaptation) experimental period. However, the utilization of Arctic cod was stable after three days feed adaptation and at a higher level than the

adaptation of capelin in the previous period. Also birds that were captured for the Arctic cod experimental period and that only had three days to adapt to being caged, had the same degree of utilization of Arctic cod as those that had been caged up to nine days. A too short adaptation period to get used to being kept in cages is therefore not very likely to be the reason for fluctuating energy utilization.

Fluctuating protein quality can result in fluctuating energy utilization (McNab and Shannon 1974). The protein concentration was, however, the same in all four feeds, with the result that the protein intake was lowest where the energy utilization was best, i.e. in the Arctic cod period. Percent nitrogen retained of the nitrogen taken in was highest for the kittiwakes in the capelin period. For thick-billed murre, no difference could be demonstrated in this "nitrogen utilization" between the two experimental periods. The "nitrogen utilization" in the (p.45) two periods can still not be considered to be equal because the average value in the capelin period was 9% higher than the value in the Arctic cod period. This means that the capelin protein could not have been quantitatively poorer than the Arctic cod protein either for the kittiwakes or the murres, and different protein quality can therefore not explain the different energy utilizations.

The nutritional differences in the feeds were the differences in fat content. The lowest fat content was found in capelin (3%) which also gave the lowest energy utilization in the two bird species. Arctic cod with 5% and 10% fat gave respectively the next highest and highest energy utilization. The relationship between the fat content in the feed and the energy utilization is illustrated in Figure 5. The figure indicates that there is a linear relationship between the energy utilization of the birds and the fat content of the feed , independent of bird species and feed type. It appears from this that kittiwakes and thick-billed murres have equally efficient mechanisms for utilizing the energy in capelin and Arctic cod if these have the

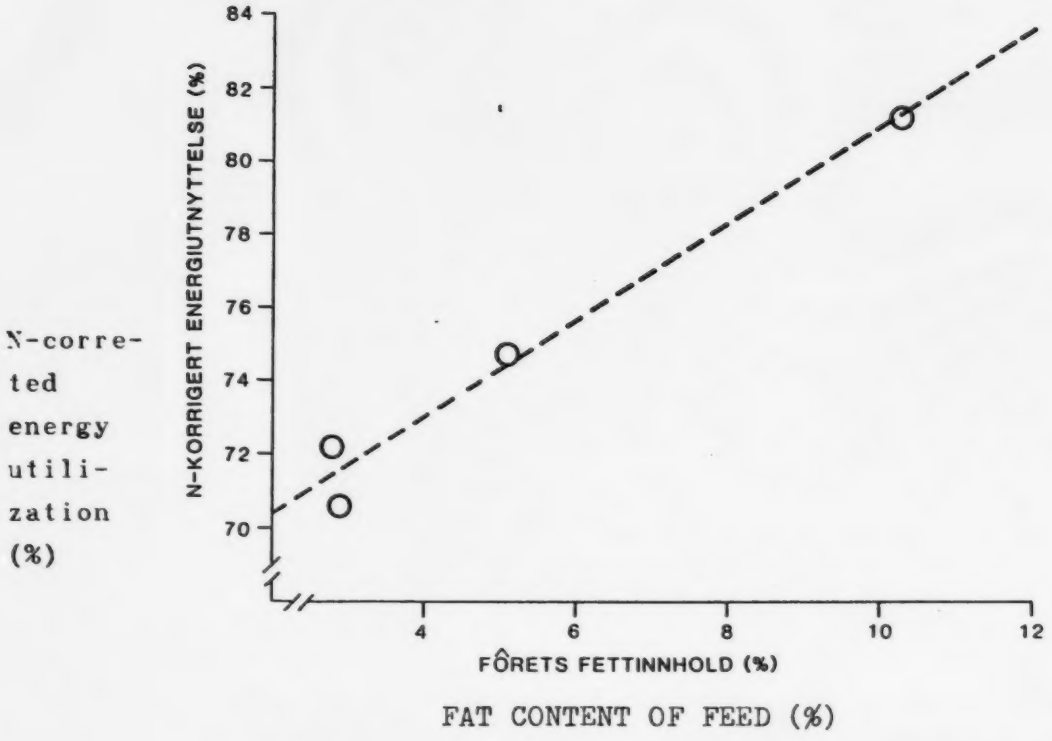



Figure 5 The relationship between the fat content of the feed (in % wet weight) and the energy utilization of the feed. The regression line y= 67.4 + 1.4x is drawn through the points.

same fat content, and that the degree of utilization varies proportionally with varying fat contents. It can be investigated if this is correct through corresponding experiments as in this study where the two bird species are fed with the same feed and the fat content in the feed is varied.

Variations in the energy utilization therefore do not appear to be a result of the physiology of the birds, but also a result of the quality of the feed. The larger part of the feed that consists of fat in relation to the other ingredients, the higher the degree of utilization appears to be. This is in agreement with earlier observations that fat is a more efficient source of energy than proteins and carbohydrates (Donato and Hegsted 1985).

Supplementation of the diet with fat has become routine in the preparation of poultry feeds. It is primarily used to increase the caloric density of the feeds (Sell and Owings 1981). Fat will in addition slow down the velocity of the passage through the digestive channel which should lead to increased time for digestion and absorption of all nutrients in the feed. The thermal energy (calorigenic effect) for fat is also lower for protein and carbohydrate.

Supplementing the feed with fat also leads to a better utilization of the feed (f.ex. Biely and March 1954, Sunde 1954); an increase that exceeds the value expected on the background of the addition of the energy from the fat (Touchburn and Naber 1966, Jensen et al 1970, Sell and Owings 1981). This was called "the extra-caloric effect of fat" by Touchburn and Naber (1966) and has since been the subject of extensive studies ( f.ex. Wilder et al 1959, Potter 1976, Hurwitz et al 1986, Maiorino et al 1986). Mateos and Sell (1980) showed that this effect can be due to synergism between saturated and unsaturated fatty acids, and increased energy utilization of the non-lipid components of the feed.

Fish (marine) fats contain both saturated and unsaturated fatty acids. In addition to the fact that an increased fat (p.47) content leads to increased energy density, it is therefore possible that fish fat exhibits a so-called extracaloric effect in seabirds, similar to the effect of several types of fat in poultry.

Several studies of the energy utilization of kittiwake and murre must be carried out in order to clarify if they really have the same degree of utilization of fish (natural food) with the same fat content, and if the degree of utilization varies with varying fat content. Studies with several other seabird species would clarify if this is general for seabirds.

### 4.2.3 Comparison of energy utilization between kittiwake, thick-billed murre and other bird species.

Jackson (1986) has studied the nitrogen - corrected energy utilization of different feeds with white-chinned petrels.

The nitrogen - corrected energy utilization of lean fish (Maurolicus muelleri; 69.1%) by white - chinned petrels is lower than kittiwake's and murre's utilization of capelin and Arctic cod. The difference is, however, slight between the energy utilization of capelin by kittiwake and murre (which in the current study is considered a lean fish) and the energy utilization of lean fish by the petrels (respectively 1.5% and 3.1%). Unfortunately, no nutrient analysis was performed in the Jackson study, but the content of energy in lean fish (20.5 kJ $g^{-1}$) is approximately the same as the energy content in the two capelin feeds in my study (20.1 kJ $g^{-1}$ and 20.8 kJ $g^{-1}$). This can reflect that the fat content is approximately the same, which can contribute to a similar degree of utilization.

Jackson has in the same study investigated the energy utilization of squid (Loligo reynaudi; 68.0%) and Antarctic krill (Euphasia superba; 67.5%) by white-chinned petrels. These are food animals with different biochemical structures from (p.48) fish, and this makes it difficult to compare these results directly with mine.

Recalculation of $TME_n$ values taken from Sibbald (1986) where the utilization of a number of different feed types by poultry were studied, shows that the nitrogen - corrected degree of utilization varies from 17.5% for whey powder to 99.4% for glucose. Other feeds that gave good utilization (over 80%) was corn waste, maize (corn), corn starch, oats, wheat and rice bran; i.e. feeds that I consider to be natural for poultry. Barley, also assumed to be a natural feed for poultry, gave a utilization between 70% and 75%. Fish meal, shrimp meal, crab meal, blood meal, bone meal, meat meal, feather meal, eggs and milk (I consider these not to be natural feeds for poultry) gave an

average degree of utilization of respectively 64.2%, 39.2%, 31.3%, 64.5%, 79.7%, 60.8%, 58.6%, 69% and 62.2%. With the exception of bone meal, all showed a relatively much lower degree of utilization than the above mentioned grains. Not only animal, but also some vegetable feeds gave a low degree of utilization, among them alfalfa (20%0, linseed (42.2%), soybeans (50%) and sunflower seeds (47%).

My results are in agreement with these values from Sibbald (1986) where "natural feeds" give an utilization of between 70% and 90%.

## 4.3 Model studies

The real situation is difficult to describe with mathematical models since the components in the systems to be described often are many and the interaction between them complicated. Reality is therefore simplified in a model.

Several models have been developed of the energy (p.49) consumption of seabirds (f.ex. Wiens and Scott 1975, Furness 1978, Furness and Barnett 1985). From the estimated energy consumption, a calculation can be made of how much this is equivalent to in tonnes of fish. In these models no consideration is given to the importance of seasonal variations in the energy content of food animals or in the calculation of their energy consumption. Instead values for the whole year are used for energy utilization and energy content in the feed based on literature values that are not average values for the year.

To take into consideration seasonal variations in the energy content of food animals, the energy consumption should be calculated for shorter periods of the year. The average energy content of the food animals for this period is then used to determine the energy utilization of the birds, and together with the energy requirements for the period to calculate their energy consumption. Energy consumption per period is then added up to give yearly energy consumption.

I will give an example of how the food consumption for the kittiwakes on Svalbard and thick-billed murres can be calculated where consideration is given to the fluctuating energy content of the feeds and the varying energy utilization by different feeds by the birds. I will look at adult, nesting birds in the month they are feeding their young. Feeding of the young takes place chiefly from the middle of July to the middle of August (30 days). I have assumed that they in this period eat only capelin or only Arctic cod.

Energy requirements of the birds.

A kittiwake of 366 g has in the period they have their young a resting metabolism of 289 kJ $day^{-1}$ (Gabrielsen et al 1988). In the same period the field metabolic rate is 558 kJ $day^{-1}$ (1.9 X the resting metabolism) when the bird is on the nest, and 926 kJ $day^{-1}$ (3.2 X the resting metabolism) when it is away from the nest (Gabrielsen et al 1987). The birds spend as much time at the nest as away from it. (p.50)

The energy requirement per kittiwake in this 30 day period then becomes:

| | | |
|---|---|---|
| 558 kJ $day^{-1}$ | x 15 days = | 8370 kJ |
| 926 kJ $day^{-1}$ | x 15 days = | 13890 kJ |
| | | 22260 kJ |

Average daily requirement is 22260 : 30 = 742 kJ.

Only the resting metabolism has been studied in thick-billed murre. Preliminary studies have, however, shown that the relationship between field metabolism and resting metabolism is approximately the same for Arctic seabird species (Gabrielsen and Mehlum, in press). Resting- and field metabolic rates for thick-billed murre is therefore calculated based on the relationship between these two values in kittiwake (sse below).

A thick-billed murre of 967 g has in the chick period a resting metabolism of 517 kJ $day^{-1}$ (Gabrielsen et al 1988). Calculated metabolism is 982 kJ $day^{-1}$ (517 kJ $day^{-1}$ x 1.9) while it is on the nest, and 1654 kJ $day^{-1}$ (517 kJ $day^{-1}$ x 3.2) while it is away from the nest. I assume that these birds also spend as much time on the nest as away from it.

The energy requirement per thick-billed murre in the period is then:

982 kJ $day^{-1}$ x 15 days = 14730 kJ
1654 kJ $day^{-1}$ x 15 days = 24810 kJ

= 39540 kJ

Average daily requirement is 39540 : 30 = 1318 kJ.

The energy value of food animals

In July/August the Arctic cod has a fat content of around 5%, corresponding to an energy content of 4.9 kJ $g^{-1}$ (wet weight). The degree of utilization of this fish by the murre was 75%. Furthermore, the degree of utilization of a feed is (p.51) approximately the same for kittiwakes and murres.

The utilizable energy in Arctic cod by kittiwakes and murres is therefore:

$$\frac{4.9 \text{ kJ g}^{-1} \times 75\%}{100} = 3.68 \text{ kJ g}^{-1} \text{ (wet weight)}$$

Capelin contain around 12% fat in July/August (Jangaard 1974), corresponding to an energy content of 7.25 kJ $g^{-1}$ (wet weight; Montevecchi and Piatt 1984).

I found that the energy utilization increased with the increasing fat content in feed, and according to Figure 5, 84% of

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the energy in capelin with a fat content of 12% will be utilizable by kittiwakes and murres.

For kittiwakes and thick-billed murres the utilizable energy in capelin is therefore:

$$\frac{7.25 \text{ kJ g}^{-1} \times 84\ \%}{100} = 6.09 \text{ kJ g}^{-1} \text{ (wet weight).}$$

Consumption of food animals.

Consumption of fish per bird in the 30-day period becomes:

Kittiwake

Arctic cod $\quad \frac{22260 \text{ kJ}}{3.68 \text{ kJ g}^{-1}} = 6049 \text{ g (ca. 200 g day}^{-1})$

or:

Capelin $\quad \frac{22260 \text{ kJ}}{6.09 \text{ kJ g}^{-1}} = 3655 \text{ g (ca. 120 g day}^{-1})$

Thick-billed murre

Arctic cod $\quad \frac{39540 \text{ kJ}}{3.68 \text{ kJ g}^{-1}} = 10745 \text{ g (ca. 360 g day}^{-1})$

or:

Capelin $\quad \frac{39540 \text{ kJ}}{6.09 \text{ kJ g}^{-1}} = 6493 \text{ g (ca. 215 g day}^{-1})$

It is estimated that around 220,000 pairs of (p.52) kittiwakes and 476,000 pairs of thick-billed murres nest on Svalbard (Bakken, personal communication). The calculated quantity consumed of capelin/ Arctic cod for these two species in one month (the chick feeding season) is shown in Table 10.

Table 10 Calculated consumption of capelin/Arctic cod around Spitsbergen and Bear Island during chick feeding season by kittiwakes and thick-billed murres.

| | Capelin | Arctic cod |
|---|---|---|
| Kittiwake | 1608 t | 2002 t |
| Thick-billed murre | 6181 t | 10229 t |
| Total | 7789 t | 12831 t |

Furness and Barrett (1985) has estimated the yearly consumption by seabirds around Hornöy and Reinöy to 9000 tonnes yearly, of which 7500 tonnes is capelin (energy utilization: 80%, energy content in feed: 5 kJ $g^{-1}$). Around 85,000 pairs of seabirds of nine different species nest on these islands. Kittiwakes and herring gulls (Larus argentatus) are most numerous, respectively 27% and 50% of the total number.

On the basis of these values from Furness and Barrett (1985), I have calculated the average food consumption per bird around Hornöy and Reinöy:

9000 tonnes : 170,000 birds = 53 kg $year^{-1}$
53 kg $year^{-1}$ : 12 months = 4.4 kg $month^{-1}$
4.4 kg $month^{-1}$ : 30 days = 147 g $day^{-1}$

This corresponds approximately to what a kittiwake needs of capelin/Arctic cod in the chick feeding season (July/August).

A herring gull weighs 600-1000 g (Haftorn 1971), i.e. two to three times more than a kittiwake, and it therefore has a higher energy requirement than the kittiwake. Since 60% of the birds in this model are herring gulls and 30% are kittiwakes, it (p.53) would appear that the above feed consumption values are somewhat low relative to the calculated feed consumption for a kittiwake in the chick feeding season. However, a direct comparison of Furness' and Barret's results with my results is difficult. The results from Hornöy and Reinöy are average values for the whole year while the values from this study are from the chick feeding season.

Very little is known about the energy requirements of seabirds in the winter season. It is generally assumed that birds have lower energy requirements in the winter than in the nesting season.

A low energy requirement in the winter can lead to a low average food demand per month (on an annual basis) if the "food" has not gone through a reduction in energy content.

The model proposed by Furness and Barrett will be more or less realistic according to what degree bird's energy requirements and the food animal's energy contents are reduced during the year.

In July/August a kittiwake need ca. 200 g Arctic cod or ca. 120 g capelin daily to cover its energy requirements. This means 55% and 33% of the body weight. A thick-billed murre requires in the same period ca. 360 g Arctic cod or 215 g capelin daily. This means 37% and 22% of the body weight.

For comparison, a ringed seal weighing ca. 45 kg has an energy intake in July/August of 28,000 kJ per day (80% digestibility; Ryg, personal communication). This corresponds to 6 kg Arctic cod or 4 kg capelin; respectively 13% and 9% of the body weight. A minke whale of ca. 7 tonnes has an average daily energy requirement of ca. 592,000 kJ (Markussen and Øritsland,

1986). With a degree of utilization of 80% this corresponds to 150 kg Arctic cod or 100 kg capelin daily; this means respectively 2% and 1.4% of the body weight. This is in accordance with the doctrine that specific metabolic rate increases with decreasing body weight (p.54) (Schmidt-Nielsen 1985). (In the calculations above the arctic cod has an energy content of 4.9 kJ $g^{-1}$ and the capelin an energy content of 7.25 kJ $g^{-1}$ ).

This means that seabirds need more food per body weight unit than seals and whales. From the example with capelin above we have:

biomass (7 tonnes):
1 minke whale = 156 ringed seals, 7239 thick-billed murres or 19126 kittiwakes.

capelin consumption per day for 7 tonnes of the various species:

| | |
|---|---|
| minke whale | - 100 kg |
| ringed seal | - 624 kg |
| thick-billed murre | - 1556 kg |
| kittiwake | - 2295 kg |

This means: 7 tonnes of ringed seals need 6 times more capelin than a minke whale,

7 tonnes thick-billed murres need 16 times more capelin than a minke whale,

7 tonnes kittiwakes need 23 times more capelin than a minke whale.

During the chick feeding season, respectively 16% and 25% of the energy in the consumed capelin and Arctic cod is returned to the environment in the form of guano. This corresponds to 9.0 x $10^9$ kJ from the capelin consumed and 1.6% x $10^{10}$ kJ from the Arctic cod consumed. Of this, respectively 1608 tonnes and 2811

tonnes are in the form of nitrogen (dry weight).

For comparison, the average field of potatoes in (p.55) Norway is fertilized with ca. 12 kg nitrogen per dekar. Each dekar yields ca. 3000 kg potatoes (Edland, Norwegian Farmers Org., personal communication). The Svalbard stock of kittiwakes and thick-billed murres could in other words in a month fertilize around 160,000 dekar potato fields that would yield ca. 480,000 t potatoes. This is as much as the yearly potato crop in Norway which is around 450,000 t (Edland, Norwegian Farmers Org., personal communication).

The capelin in the Barents Sea has for many years been an important commercial fish species. The estimated capelin stock (2 years and older) has declined by 99% in the period 1980-1987, from 5.5 million tonnes to 20,000 tonnes ( Fisken og Havet, Special Issue 1, 1987 (Inst. Mar. Res.,Bergen)). However, during 1988 the estimated capelin stock has grown to around 400,000 tonnes. Earlier Norwegian fishermen harvested up to 2.9 million tonnes capelin a year, but the fishery for capelin has now been stopped since 1987 (Fisken og Havet, Special Issue 1, 1988; Gjösether, personal communication).

The stocks of Arctic cod were probably small around 1970, when the fishery for this species was heavy, but they have since increased as the fishery has declined. The Arctic cod stocks in the Barents Sea were estimated to be 590,000 tonnes in 1987, but had an estimated drop in 1988 to 130,000 tonnes (Fisken og Havet, special issue 1, 1988; Gjösether pers. comm.).

The calculated consumption of respectively capelin and Arctic cod by kittiwakes and murres in a summer month is 2% and 10% of the observed capelin- and Arctic cod stocks in the Barents Sea in 1988.

Birds and sea mammals move over limited areas in search of food. This results in local effects where fish and fish consumers affect each other. For example, in years with little fish around the nesting colonies the seabirds will not be able to feed their young, and reproduction will be low. In years will little

available fish in the sea it will be difficult for (p.56) seabirds to survive the winter. As example we can mention the starvation observed among the capelin specialist, the common murre (Uria aalge) in the winter of 1987 (Bakken, personal communication).

In contrast to the sea animals, people have such efficient harvesting - and transportation methods that they can regulate most animal stocks, not only locally, but globally. In addition , instruments have been developed to quantify the amount of fish in the sea. From earlier experiences we also know something about how much exploitation a fish stock can take without being reduced. We still do not know the number of, and the nutritional requirements for,all consumers in the ocean, but preliminary estimates are available for many species. It therefore appears that we now are in the situation that we can determine the future of the ecosystem the Barents Sea through our management of the resources in the Barents Sea.

## 4.4 Conclusion

Nitrogen-corrected energy utilization was for kittiwakes and thick-billed murres respectively 72.2% and 70.6% for capelin feed and 81.2% and 74.7% for Arctic cod feed.

The fluctuating fat(energy) content could have been the reason for the variations in energy utilization. It has earlier been shown that the addition of fat in feed can give increased energy utilization. This is due to the fact that fat in general increases the energy density of a feed, that fat lowers the velocity of food passage through the digestive tract, that fat has low calorigenic effect and that fat has a so-called extra calorific effect that is often seen when supplementing feed with fat.

The nesting kittiwakes and thick-billed murres at (p.57) Svalbard can in the chick feeding season (30 days) consume 7789 tonnes capelin or 12891 tonnes Arctic cod. This is respectively

2% and 10% of the capelin- and Arctic cod stocks in the Barents Sea in 1988.

Per body weight unit, kittiwakes and thick-billed murres need respectively 23 and 16 times more capelin than minke whales in order to cover their daily energy requirements.

During the chick feeding season, respectively 16% ($9.0 \times 10^9$ kJ) and 25% ($1.6 \times 10^{10}$ kJ) of the consumed energy in capelin/ Arctic cod is returned to the environment around the colonies in the form of guano. This amount of guano contains respectively 1608 tonnes and 2811 tonnes of nitrogen.

# LITTERATUR

Adams, N.J., 1984: Utilization efficiency of a squid diet by adult king penguins (Aptenodytes patagonicus). Auk. 101: 884-886.

Belopol´skii, L.O., 1957: Ecology of sea-colony birds of the Barents Sea. Oversatt fra russisk, 1961. Israel Prog.Sci.Transl., Jerusalem.

Biely, J. og March, B., 1954: Fat studies in poultry. 2. Fat supplements in chick and poult rations. Poltry. Sci. 33: 1220-1227.

Brown, G.B. og Nettleship, D.N., 1982: Capelin and seabirds in the northwest Atlantic. I Marine birds: their feeding ecology and commercial fisheries relationship. Eds. D.N. Nettleship, G.A. Sanger og P.F. Springer. Proc. Pac. Seabird gr. Symp.: 184-194.

Cooper, J., 1977: Energetic requirements for growth of the jacass penguin. Zool. Afr. 12: 201-213.

Cooper, J., 1978: Energetic requirements for growth and maintenance of the Cape gannet (Aves; Sulidae). Zool. Afr. 13: 305-317.

Cooper, J., 1980: Energetic requirements for maintenance of a captive juvenile great white pelican Pelecanus onocrotalus. Cormorant 8: 17-19.

Cramp, S. (Ed.), 1983: Handbook of the birds of Europe, the Middle East and North Africa: the birds og the Western Palearche. Vol. 3. Oxford University Press, Oxford.

Crawford, R.J.M. og Shelton, P.A., 1978: Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. Biol. Conserv. 14: 85-109.

Croxall, J.P., 1983: Seabirds. I Antarctic ecology. Vol. 2. Ed. R.M. Laws. Academic Press, London.

Donato, K. og Hegsted, D.M., 1985: Efficiency of utilization of

various sources of energy for growth. Proc. Natl. Acad. Sci. 82, V: 4866-4870.

Dunn, E.H., 1975: Caloric intake of nestling double-crested cormorants. Auk 92: 553-565.

Eaton, C.A., Ackman, R.G. og Tocher, C.S., 1975: Canadian capelin 1972-1973. Fat and moisture composition, and fatty acids of some oils and lipid extract triglycerides. J. Fish. Res. Board Can. 32: 507-513.

Eurola, S. og Hakala, U.K., 1977: The bird cliff vegetation of Svalbard. Aquilo Ser. Bot. 15: 1-18.

FAO/WHO, 1973. Energy and protein requirements.

Fisken og havet 1988. Særnummer 1. Ed. E. Bratberg. Rapporter og meldinger fra Fiskeridirektoratets Havforskningsinstitutt - Bergen.

Furness, R.W., 1978: Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47: 39-53.

Furness, R.W. og Barrett, R.T., 1985: The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scand. 16: 305-313.

Gabrielsen, G.W., Mehlum, F. og Nagy, K.A., 1987: Daily energy expenditure and energy utilization of the free-ranging black-legged kittiwakes. Condor. 89: 126-132.

Gabrielsen, G.W., Mehlum, F. og Karlsen, H.E., 1988: Thermoregulation in four species of arctic seabirds. J. Comp. Physiol. B 157: 703-708.

Gabrielsen, G.W. og Mehlum, F., 1989: Thermoregulation and energetics of arctic seabirds. I Physiology and adaptions to cold in birds. Eds. R. Reinertsen og C. Bech. Plenum Press. (in press).

Gjertz, I., Mehlum, F. og Gabrielsen, G.W., 1985: Food sample analysis of seabirds collected during the 'Lance'-cruice in ice-filled

waters in Eastern Svalbard 1984. Norsk Polarinstitutt Rapport-serie Nr. 23.

Haftorn, S., 1971: Norges fugler. Universitetsforlaget.

Harris, L.E., 1966: Biological energy interrelationships and glossary of energy terms. Publ. 1411, National Academy of Sciences, Washington, D.C.

Harris, M.P. og Birkhead, T.M., 1985: Breeding ecology of the Atlantic Alcidae. I The Atlantic Alcidae. Eds. D.N. Nettleship og T.R. Birkhead.

Heath, R.G.M. og Randall, R.M., 1985: Growth of jackass penguin chicks (Spheniscus demersus) hand reared on different diets. J. Zool., Lond. (A) 205: 91-105.

Holm, H., Hustvedt, B.E. og Løvø, A., 1973: Protein metabolism in rats with ventromedial hypothalamic lesions. Metabolism. 22: 1377-1387.

Hunt Jr., G.L., Burgeson, B. og Sanger, G.A., 1981: Feeding ecology of seabirds of the Eastern Bering Sea. I The Eastern Bering Sea Shelf: Oceanography and Resources. Vol. 2. Eds. D.W. Hood og J.A. Calder.

Hurwitz, S., Plavnik, I., Bengal, I. og Bartov, I., 1986: Response of growing turkeys to dietary fat. Poultry Sci. 67: 420-426.

Jackson, S., 1986: Assimilation efficiencies of white-chinned petrels (Procellaria aequinoctialis) fed different prey. Comp. Biochem. Physiol. 85A: 301-303.

Jangaard, P.M., 1974: The capelin (Mallotus villosus). Biology, distribution, exploitation, utilization and composition. Bull. Fish. Res. Board Can. 186.

Jensen, L.S., Schumaier, G.W. og Latshaw, J.D., 1970: "Extra caloric" effect of dietary fat for developing turkeys as influenced by calori-protein ratio. Poultry Sci. 49: 1697-1704.

Klekowski, R.Z. og Opalinski, K.W., 1986: Matter and energy flow in Spitsbergen ornithogenic tundra. Polar Research 4 n.s.: 187-197.

Kooyman, G.L., 1989: Behavior and physiology of diving in emperor and king penguins. I International Conference on the biology of penguins New Zeeland, 1988. (maunskript).

Lydersen, C., Gjertz, I. og Weslawski, J.M., 1985: Aspects of vertebrate feeding in the marine ecosystem in Hornsund, Svalbard. Norsk Polarinstitutt Rapportserie Nr. 21.

Maiorino, P.M., Al-Hozab, A.A., Mitchell, R. og Reid, L., 1986: Animal fat effects on nutrient utilization. Poultry Sci. 65: 2304-2313.

Markussen, N.H. og Øritsland, N.A., 1986: Vågehval. Internrapport, Avd. for generell fysiologi, Universitetet i Oslo.

Mateos, G.G. og Sell, J.L., 1980: Influence of carbohydrate and supplemental fat source on the metabolizable energy of the diet. Poultry Sci. 59: 2129-2135.

McNab, J.M. og Shannon, D.W.F., 1974: The nutritional value of barley, maize, oats and wheat for poultry. Br. poult. Sci. 15: 561-567.

Mehlum, F, og Gjertz, I., 1984: Feeding ecology of seabirds in the Svalbard area - a preliminary report. Norsk Polarinstitutt Rapportserie Nr. 16.

Miller, M.R. og Reinecke, K.J., 1984: Proper expression of metabolizable energy in avian energetics. Condor 86: 396-400.

Montevecchi, W.A. og Piatt, J., 1984: Composition and energy contents of mature inshore spawning capelin (Mallotus villosus): implications for seabird predators. Comp. Biochem. Physiol. 1: 15-20.

Norderhaug, M., 1970: The role of the little auk, Plautus alle (L.), in arctic ecosystems. Antarctic ecology 1: 558-560.

Norderhaug, M., Brun, E. og Uleberg Møllen, G., 1977: Barentshavets sjøfuglressurser. Norsk Polarinstitutt Meddelelser Nr. 104.

Potter, L.M., 1976: Fat in turkey diets: How much it´s worth. Turkey World 51: 6-8.

Pro Mare (marinøkologisk forskningsprogram i Arktis) årsrapport 1984. Trondheim.

Pro Mare årsrapport 1985. Trondheim.

Pro Mare årsrapport 1986. Trondheim.

Pro Mare årsrapport 1987. Trondheim.

Remmert, H., 1980: Arctic animal ecology. Springer-Verlag.

Schmidt-Nielsen, K., 1985: Animal physiology. Cambridge University Press.

Schneider, D. og Hunt Jr., G.L., 1982: A comparison of the seabird diets and foraging distribution around the Pribilof Islands, Alaska. I Marine birds: their feeding ecology and commercial fisheries relationships. Eds. D.N. Nettleship, G.A. Sanger og P.F. Springer. Proc. Pac. Seabird gr. Symp.: 86-95

Sell, J.L. og Owings, W.J., 1981: Supplemental fat and metabolizable energy-to-nutrient ratios for growing turkeys. Poultry Sci. 60: 2293-2305.

Sibbald, I.R., 1982: Measurement of bioavailable energy in poultry feedingstuffs: a review. Can. J. Anim. Sci. 62: 983-1048.

Sibbald, I.R., 1986: The T.M.E. system of feed evaluation: methodology, feed composition data and bibliography. Agriculture Canada, Tech. bull 1986-4E.

Sunde, M.L., 1954: The use of animal fats in poultry feeds. J. Amer. Oil Chem. Soc. 31: 49-52.

Titus, H.W., Mehring Jr., A.L., Johnson Jr., D., Nesbitt, L.L. og Tomas, T., 1959: An evaluation of MCF (Micro-Cell-Fat), a new type of fat product. Poultry Sci. 38: 1114-1119.

Touchburn, S.P. og Naber, E.C., 1966: The energy value of fats for growing turkeys. Proc. 13th World´s Poultry Congr., Kiev, USSR:

190-195.

Tuck, L.M., 1960: The Murres: their distribution, populations and biology - a study of the genus Uria. The Queen's Printer, Ottawa.

Whittow, G.C., 1986: I Avian physiology. Ed. P.D. Sturkie. Springer-Verlag

Wiens, J.A. og Scott, J.M., 1975: Model estimation of energy flow in Oregon costal seabird populations. Condor 77: 439-452.

Wilder, O.H.M., Cullen, M.P. og Rasmussen, O.G., 1959: Metabolizable energy values of different types and grades of fats in practical chick diets. Poultry Sci. 38: 1259-1260 (abstr.).

Wolynetz, M.S. og Sibbald, I.R., 1984: Relationship between apparent and true metabolizable energy and the effects of a nitrogen correction. Poultry Sci. 63: 1386-1399.

## LITERATURE

Fisken og Havet (The Fish and the Ocean) 1988. Special Issue 1. Editor E. Bratberg. Reports and Notices from the Directorate of Fisheries Institute of Marine Research- Bergen.

Haftorn, S., 1971: The Birds of Norway. University Publishers.

Markussen, N.H. and Øritsland, N.A., 1986. Minke whale. Internal Report, Div. for General Physiology, the University in Oslo.

Norderhaug,M., Brun, E. and Uleberg Möllen, G., 1977: The Seabird Resources in the Barents Sea. Norwegian Polar Institute Reports No. 104.

Pro Mare (Marine Ecological Research Program in the Arctic) Annual Report 1984. Trondheim.

## APPENDIX 1

Two-way Mann-Whitney U-test for all combinations of the groups (bird/feed) on the carbon-, nitrogen- and energy content values in the guano gave the following results:

Guano: CARBON

| | kittiwake/ Arctic cod | thick-billed murre/ capelin | thick-billed murre/ Arctic cod |
|---|---|---|---|
| kittiwake/ Arctic cod | SIGNIFICANT | | |
| thick-billed murre/ capelin | TENDENCY | NOT SIGNIFICANT | |
| thick-billed murre/ Arctic cod | NOT SIGNIFICANT | SIGNIFICANT | TENDENCY |
| | kittiwake/ capelin | kittiwake/ Arctic cod | t.b.murre/ capelin |

Guano:NITROGEN

| | kittiwake/ Arctic cod | t.b.murre/ capelin | t.b.murre/ Arctic cod |
|---|---|---|---|
| kittiwake/ Arctic cod | TENDENCY | | |
| t.b.murre/ capelin | TENDENCY | NOT SIGNIFICANT | |
| t.b.murre/ Arctic cod | NOT SIGNIFICANT | TENDENCY | NOT SIGNIFICANT |
| | kittiwake/ capelin | kittiwake/ Arctic cod | t.b murre/ capelin |

Guano: Energy

| | | | |
|---|---|---|---|
| kittiwake/ Arctic cod | SIGNIFICANT | | |
| t.b. murre/ capelin | SIGNIFICANT | SIGNIFICANT | |
| t.b.murre/ Arctic cod | SIGNIFICANT | NOT SIGNIFICANT | NOT SIGNIFICANT |
| | kittiwake/ capelin | kittiwake/ Arctic cod | t.b murre/ capelin |